FISH OBLIQUE TO BEDDING IN EARLY DIAGENETIC CONCRETIONS FROM THE CRETACEOUS SANTANA FORMATION OF BRAZIL – IMPLICATIONS FOR SUBSTRATE CONSISTENCY

by david M. Martill

ABSTRACT. A large number (> 1 per cent.) of fossil fish from the Santana Formation (?Albian, Lower Cretaceous) of north-east Brazil, occurs at a high angle, or even vertical, to bedding. Petrographic and taphonomic analyses of such occurrences indicate that the laminated argillaceous sediments were soupy and allowed sinking dead fish to penetrate the sediment to depths greater than the total body length of the fish. Density contrasts between the dead fish and the surrounding sediment were negligible, and penetration was largely a result of acceleration due to the high density contrast between the fish and the water column. A commonly recurrent angle of fish to bedding of approximately 45° reflects the gliding angle achieved during forward descent with pectoral fins extended.

CONCRETIONS containing exceptionally well preserved fish from the Romualdo Member of the Santana Formation are extremely abundant on the slopes of the Chapada do Araripe, in the states of Ceará, Pernambuco and Piauí, north-east Brazil (Martill 1993*a*). At several localities around the plateau (Text-fig. 1), fossil fish occur preserved in three dimensions and at a high angle to the bedding in early diagenetic, calcium carbonate concretions. Such a specimen was first illustrated by Martill (1988), and many more were figured by Maisey (1991). Maisey recognized two concretions types where fossils lay at an angle to the bedding. In one (his type 'K' transgressive concretions) the entire fish lies oblique to bedding, whereas in the second type (his type 'I' partly transgressive concretions) only the skull lies oblique to bedding, the remainder of the fish lying parallel to the bedding plane. He also noted that the first type of concretion contained mostly specimens of *Rhacolepis*, whereas the second type of concretion contained mostly large specimens of *Rhacolepis*, whereas the second type of concretion contained mostly large specimens of *Cladocylus gardneri*, *Enneles audax* (= *Calamopleurus cylindricus*) and *Araripelepidotes tennurus* also occur commonly in type 'I' concretions.

Two distinct hypotheses have been advanced to explain these occurrences (Maisey 1991, p. 67). The model proposed for the type 'I' concretions is accepted herein and I merely make a few additional observations. However, I offer an alternative explanation for the generation of type 'K' concretions based on observations of new specimens using thin section petrography, and on extensive field observations.

Specimens are housed in the following institutions: FMNH, Field Museum of Natural History, Chicago; LEIUG, University of Leicester, Department of Geology; UOP, University of Portsmouth, Department of Geology.

SEDIMENTOLOGY OF THE CONCRETION HORIZON

The Romualdo Member concretions occur in a series of grey-green to dark grey, laminated, slightly silty mudstones which were deposited in a restricted lagoon with connections to an epeiric sea. The muds are composed of approximately 75 per cent. smectite, 20 per cent. illite and 5 per cent.

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TEXT-FIG. 1. Simplified map of the eastern end of the Chapada do Araripe (shaded area), Brazil, with the main fossil bearing concretion localities indicated by a fish symbol. Localities discussed in the text are: a, Mina Pedra Branca, b, Serra da Maozina.

kaolinite (Berthou *et al.* 1990). The member rarely reaches more than 4–5 m thick, but is laterally extensive occurring over an area of at least 6000 km². Ostracods are abundant at some horizons and may even produce thin, impersistent, ostracodal limestones. Septarian concretions occur at intervals, sometimes in discrete bands, but some also appear to be randomly distributed. The concretion-bearing part of the sequence rests on a series of fluviodeltaic and lacustrine sands and silts, with palaeosols and rootlet horizons. The Romualdo Member passes upwards into slightly micaceous, blue/grey shales with thin bands of gastropod limestone rich in *Paraglauconia* and with rare echinoids.

The palaeosalinity of the concretion-bearing part of the sequence is in doubt, but deposition was probably under rather brackish conditions (Martill 1993*a*). It is highly likely that salinities fluctuated considerably with the seasons, a hypothesis based on the presence of mass mortality assemblages of young fishes. Many of the fish species found in the concretions have been reported from coeval fully marine deposits elsewhere (Moody and Maisey 1994). The salinity has important implications, both for palaeoenvironmental interpretations of the fauna and also for the behaviour of the sediment, as salinity plays an important rôle in clay particle flocculation (see below).

THE CONCRETIONS

The concretions containing fish skeletons preserved oblique to bedding are irregularly ellipsoidal, and commonly range from 150 to 400 mm long by 50 to 150 mm wide. The outer surface of the concretion is commonly weathered light brown, with a friable, highly oxidized zone rich in selenite

crystals which readily breaks away from the main body of the concretion. Lamination is conspicuous on the weathered surface, but is enhanced after light etching in 10 per cent, acetic acid. The unweathered concretions from Serra da Maozina (Text-fig. 1) are dark grey internally and are usually devoid of other fossils, whereas those from Santana do Cariri are usually a lighter grey and commonly contain coprolites, some with ostracod inclusions. These colour differences probably reflect differing degrees of weathering, rather than any lithological difference between localities. In many concretions laminations cut across the long axes of the concretions, commonly at an angle of 30-45°. In hand specimens laminations are more pronounced in concretions from Santana do Cariri than those collected from Serra da Maozina (Text-fig. 2), but etching with 10 per cent. acetic acid shows that laminations are present in all of these. Cut or split concretions commonly reveal an enclosed fish which is always three-dimensional if the fish is at a high angle (> 20°) to the bedding. but often shows collapse features if the fish is at a low angle ($< 20^{\circ}$) to bedding (Text-fig. 3). In all of the three dimensional specimens, the body cavity of the fish is filled with calcite cements and crystal-lined cavities are often present (Text-fig. 4). Laminations within the concretion body vary in thickness from 1 to 4 mm, and thicker laminae may be present. The laminae are often discontinuous, and may be flexed over and under inclusions such as coprolites (Text-fig. 5). Laminae may reach the body wall of the fish, but there is usually a zone of homogenous sediment between the laminated part of the concretion body and the body wall (Text-fig. 6). This zone is best developed in front of the skull and is often wider around the caudal region of the fish. The axial skeletons of three-dimensional fish may be articulated, but often are disarticulated. When disarticulated, the axial skeleton is often geopetally stacked (Text-figs 4A, 7). The mouth of the fish may be open and infilled with homogenous sediment (Text-fig. 2A-B) and sediment may also be present within the body of the fish and in the gill arches (Text-fig. 2B).

TAPHONOMY OF OBLIQUE FISH

Specimens of *Rhacolepis* preserved oblique to concretion laminae are invariably complete, with the body wall often preserved in three-dimensions over most of its length. The body wall is commonly ruptured, usually along spiralled scale row boundaries, and portions of the body wall and the vertebral column may be telescoped over each other (Text-fig. 7). In most cases, where such ruptures have occurred, sheets of scales have been inserted into the anterior scale row. This may occur in several places on the body, but is usually more common anteriorly. At the point of rupture, sediment may extend into the body cavity (Text-fig. 8; see also Martill 1988, pl. 4, fig. 1a–b). Sediment within the body cavity can have a very sharp boundary with later calcite infills (Text-fig. 4A–B), but in some cases the boundary is irregular, or somewhat diffuse (Text-fig. 8).

The extremities of the enclosed fish may project beyond the concretion boundary, but in most cases it is only the most anterior part of the skull and the distal parts of the caudal fins that do so. As no specimen described herein was observed by the author *in-situ* the preservational style of portions of the skeleton that lay beyond the concretion boundary cannot be documented. Specimens of fish found in the same shales as the concretions, but not enclosed within the concretions are usually highly compressed.

The pectoral and pelvic fins may extend beyond the body, as in life position, but are usually folded back somewhat (Text-fig. 9E), and the dorsal fin is often preserved in the raised position (Text-fig. 10). The strongly forked caudal fin may be slightly closed, but is planar and extends posteriorly from the caudal peduncle as in life. The mouth may be open or closed. The opercula are usually preserved flat against the skull, although in some specimens they may be open (Text-fig. 11). Anteriorly, the body wall cross section is usually nearly round and entire, but posteriorly it may be flattened with opposite sides (upper and lower surfaces) pressed into each other. Even in the most three-dimensional specimens there is usually some indication of flattening of the body wall (Text-fig. 12).

Internally, the skeleton may be fully articulated, especially within the skull, and even the finest gill rays may remain attached to the gill arches (Text-figs 3, 10). The postcranial skeleton may show

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TEXT-FIG. 2. Near complete, three-dimensional, partially articulated fish, cf. *Rhacolepis* sp. (LEIUG 110562), enclosed in an early diagenetic carbonate concretion from the Romualdo Member, Santana Formation of Santana do Cariri, Brazil. The skeleton is at a high angle to bedding with the skull pointing downwards. A, entire concretion showing complete fish with damaged dorso-lateral region revealing large gas-filled body cavity, $\times c$. 0·4. B, detail of skull showing sediment-filled mouth and fractured suboperculum exposing sediment-filled gill chamber (arrowed); $\times 1.2$.

marked disarticulation where isolated bones or sections of the postcranial skeleton have fallen away from their original position (Text-figs 3, 6, 8). Martill (1988) and Maisey (1991) noted that this skeletal collapse was often geopetal (Text-figs 4A, 7). Within the fishes, soft tissues are commonly preserved as replications in calcium phosphate (Martill 1988, 1994), and are particularly well mineralized adjacent to the body wall and in the gills (Martill *et al.* 1992; Wilby 1993). A phosphatic coeleolite is commonly present in the gut trace (Maisey 1991; Kellner *et al.* 1994; Text-fig. 10). Stomach contents, usually arthropods and smaller fishes (Wilby and Martill 1992), may also be present in fish preserved oblique to bedding (Text-fig. 13). I have found no evidence of predation or scavenging of the oblique fish (they are about as perfectly preserved specimens as one could hope to find), and the cause of death remains a topic for investigation. The high local abundance is suggestive of mass mortality.

Three dimensional fish sub-parallel to bedding. A significant number of three-dimensionally preserved fishes in the concretions are found sub-parallel to the lamination. Nevertheless, careful examination reveals laterally cross-cutting relationships with the laminae (Text-fig. 3) and many of the features described above are to be seen. Maisey (1991) described a number of fish in which only



TEXT-FIG. 3. Median longitudinal section through anterior portion of trunk (partially collapsed) and skull (three-dimensional) of cf. *Rhacolepis* sp. (UOP 96/1), block e of Text-figure 9, from the Romualdo Member, Santana Formation, Serra da Maozina, Ceará, Brazil. The lower margin reflects the original shape of the body wall of the fish, whereas the upper margin in the trunk region has collapsed geopetally following the escape of decomposition gases and the collapse internally of the supporting skeleton. A faint trace of the sediment lamination can be seen flexing down to occupy the space vacated by the escaping gases (note that the more prominent band, arrowed, is a liesegang effect produced during Recent weathering).

the head was oblique to bedding while the trunk lay parallel to the lamination. He attributed this occurrence to collapse of the body onto the sediment surface after partial intrusion of the skull into the sediment. A comparable mode of preservation has been reported for ichthyosaurs from the Posidonia Shales (Lower Jurassic) of Germany (Martill 1993b). In the case of the Santana fishes, the skull is commonly at a low angle to the bedding (although high angle examples are known; P. Wilby, pers. comm.) and upside down. Although this relationship may reflect a low angle of entry as the carcass intruded the sediment, it may also be due to post-intrusion rotation of the skull caused by leverage as the body collapsed.

DIAGENESIS

The diagenesis of fish in the concretions of the Romualdo Member has been discussed by Martill (1988). Several generations of carbonate cement fringe the bones, the earliest of which is also the cementing agent of the concretion. These cements are light grey or buff coloured and rarely reach a thickness of more than 2 mm (Text-fig. 4B). This layer may be overlain by a brownish drusy calcite cement reaching a thickness of 2–3 mm. A much thicker layer of black calcite overlies these cements and may fill all available void space (Text-fig. 4A). However, many specimens have vuggy cavities in which this black cement forms small dog-tooth crystals (Text-fig. 2). Some concretions with large vuggy cavities may contain an even later infill of coarsely crystalline white or clear calcite. Barite and celestine may also be present (Martill 1988) (Text-fig. 10). The generally bluish-dark grey colour of the concretions at Serra de Maozina is due to minor amounts of finely disseminated pyrite.

The relationship of the early cements to ingressed sediment is noteworthy. Some sediment within the body cavity appears to overlie some of the calcium phosphate replacing soft tissues. This may represent sediment that was deposited onto soft tissues that were subsequently phosphatized, but



TEXT-FIG. 4. Longitudinal section through a three-dimensionally preserved specimen of cf. *Rhacolepis* sp. (UOP 96/2), from the Santana Formation, Romualdo Member of Mina Pedra Branca, Ceará. See also Text-figures 5–6. A, complete section showing fine-scale lamination within the early diagenetic carbonate concretion, collapsed internal skeletal elements with overgrowths of calcite and larger coarse calcite crystals (dark appearance) filling the body cavity; the lower arrow shows a broad zone of unlaminated sediment in front of the fish skull; the upper arrow shows that laminations extend to the body wall and are deflected downwards slightly; $\times c$. 0-5. B, non-laminated sediment inclusion within body cavity fringed with early cement; $\times 8$.

at least some may have been deposited onto soft tissue which had already undergone very early phosphatization (Wilby 1993).

MODELS TO ACCOUNT FOR FISH PRESERVED OBLIQUE TO BEDDING

Existing model for type 'K' concretions (Maisey 1991). Maisey (1991, pp. 76–78) figured a number of examples of three-dimensional fish preserved oblique to bedding and interpreted this occurrence as a result of the fish becoming bloated due to a build up of decomposition gases and then sinking to the bottom. Maisey considered that retention of three-dimensionality was a result of early calcification of the soft tissues. He also argued that a protracted period of burial of the fish lying on the bottom 'end up' was required (Maisey 1991, p. 78). Thus, in the Maisey model, the soft tissues of the fish must effectively be fossilized and all skeletal elements, notably the scales and soft fin-ray segments, must be bound to the carcass to prevent any disarticulation occurring while awaiting burial. Further, it must be assumed that no scavenging took place. Although it is perfectly plausible to explain a lack of macro-scavenging by invoking anoxia, anaerobic bacteria can certainly



TEXT-FIG. 5. Detail of UOP 96/2 (for details see Text-fig.4) showing small coprolite with ostracod inclusions, in which laminated sediment drapes over and under the coprolite. This is a characteristic feature of elements that fell to the lagoon floor, but did not penetrate the sediment; $\times c$. 3.

operate under such conditions and cause decay (Allison 1988). Furthermore, the presence of disseminated pyrite clearly attests to the presence of sulphate-reducing bacteria. It should also be noted that there are no primary sedimentary structures, such as sediment shadows or attenuation of laminae at high points, indicating that sedimentation occurred around an object projecting from the bottom.

Other taphonomic features are also incompatible with Maisey's model. A bloated fish carcass would only float until the body wall was ruptured. Thus, three-dimensionality due to bloating was probably achieved on the lagoon floor, but failed to refloat the carcass. Not all of the three dimensional oblique fish show phosphatization of the soft tissue, and those that do often only have small areas of soft tissues preserved. Those fishes that do show extensive soft tissue preservation are often flattened (see Martill 1988, pl. 1).

The mud-dive model. Clearly, the exceptional preservation of such fossils requires an explanation. It is evident that the fish were arriving on the sea floor intact and that they underwent burial before any scavenging could occur. Scavenging could have been prevented by: (1) exclusion of macroscavengers by conditions such as hypersalinity or bottom water anoxia; and/or (2) sinking of the carcass into extremely soft (soupy) sediment. The existence of anoxic conditions on the lagoon floor was probably of frequent occurrence as infaunal benthos is exceedingly rare in the concretion layers and disseminated pyrite is abundant. The degree to which anoxicity extended upwards into the water column is unclear. Certainly, benthic invertebrates are uncommon and are usually restricted to a few horizons where small bivalves are often found in high density, but low diversity (1–2 spp.). However, this low diversity may be due to other factors, because benthic fish with high oxygen demands, such as the elasmobranchs *Iansan* and *Tribodus*, as well as some presumed benthic



TEXT-FIG. 6. For caption see opposite.

TEXT-FIG. 7. Skull and anterior portion of the trunk of cf. *Rhacolepis* sp. (UOP 96/3) in dorsal view enclosed in a carbonate concretion at an angle of 25° to the bedding; Santana Formation, Romualdo Member (?Albian, Lower Cretaceous) of the Santana do Cariri area; the body wall behind the skull has collapsed and 'sheets' of scales, arrowed,

have telescoped anteriorly; $\times 1.2$.



osteichthyans with durophagous dentitions (for example, the pycnodonts *Neoproscinetes* and *Iamanja*) occur quite commonly. Salinities may also have reached high levels, and although no evaporites are reported from this part of the succession, they are important in subjacent parts of the sequence. Even if elevated salinities and anoxia did occur, these factors alone cannot account for the unusual attitude of the fish in the concretions.

The presence of intact laminae extending almost to the body wall of the carcass, with no thickening or thinning of the laminae in the region of the fish, shows that the fish did not influence the nature or style of the accumulating sediment. The sharp truncation of the laminae where they

TEXT-FIG. 6. A, magnified contact between the body wall of the fish and the sediment in UOP 96/2 (for details see caption to Text-fig. 4). Note that the laminae are not in contact with the body wall; rather there is a zone of fluidized sediment of variable thickness between the laminated portion of the concretion and the fossil inclusion. The light material between the scales (arrowed) is phosphatized dermis; $\times c$. 3. B, outline diagram of A, highlighting features alluded to in the text.



TEXT-FIG. 8. Cut surface of block c of Text-figure 9. The lower surface of the body wall of the fish is intact, but the upper surface has collapsed geopetally. Non-brittle failure of the trunk scales internally resulted in the parting of the body wall (white arrow) from the surrounding sediment (black arrow opposite). This occurred with little or no deformation of the sediment, suggesting that the sediment was not behaving in a fluid manner when the body wall collapsed. Fluidized deformation of sediment on the right side of the body wall has occurred (black arrows to right), in which all primary lamination has been disrupted; ×4.

do meet the body wall is convincing evidence of intrusion of the fish into the sediment. The thin zone of homogenized sediment anterior to the fish skull, within the mouth and adjacent to the body, clearly shows that the fine lamination had been disrupted in the vicinity of the fish. For this to occur the sediment must have behaved in a fluid manner, but only for a short period.

A chronology of taphonomic and diagenetic events. It is usually assumed that the fish in the concretions died within the water column and sank as a dead carcass, but it is also possible that some may have died within the sediment, perhaps burrowing as a response to stress, as do some lungfishes, such as *Protopterus* and *Lepidosiren* (Bannister 1987). For those fish that did die in the water column, death was followed by at most only a very short post-mortem drifting phase, as floating carcasses decay, and rapidly disarticulate (Schäfer 1972). The lack of scavenging of the three-dimensional fish is also indicative of a very short period of post-mortem drifting. The dead fish descended (in many examples, upside down) like a glider to the floor of the lagoon, but at a steep angle of descent (around 45° in some examples). On hitting the soft substrate, the fish penetrated

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TEXT-FIG. 9. Three-dimensionally preserved, collapsed skeleton of cf. *Rhacolepis* sp. (UOP 96/1) within early diagenetic carbonate concretion; Romualdo Member, Santana Formation, Serra da Maozina, Ceará, Brazil; viewed ventrally; ×0.75. Note that the pectoral fins project out from the body wall (arrowed) indicating lithification before compaction; had compaction occurred prior to lithification the fins would have become pressed against the body. This specimen has been cut to reveal the internal sedimentary and taphonomic features shown in Text-figures 3 and 8.



TEXT-FIG. 10. Longitudinal cross section through a specimen of cf. *Rhacolepis* sp. (UOP 96/4) from the Romualdo Member, Santana Formation, Serra da Maozina, Ceará, Brazil. Note that the dorsal fin projects into the sediment, and has not been folded posteriorly during penetration into the sediment (broad arrow). There is a large phosphatic coeleolite in the gut (upper thin arrow) and a baryte infill in the skull (lower thin arrow); $\times c$. 1.



TEXT-FIG. 11. cf. *Rhacolepis* sp. (UOP 96/5) in typical Romualdo Concretion from Santana do Cariri. Note the opercula in slightly open position and the telescoping of the body wall. The open opercula might suggest that the fish was still alive when it penetrated the sediment, and that as the opercula were opened during breathing, fluidized sediment invaded the buccal cavity. $\times c$. 1.5.



TEXT-FIG. 12. Thin section of cf. *Rhacolepis* sp. (FMNH PF 10765) cut vertically through the trunk; from the Romualdo Member of the Santana Formation, precise locality unknown. Note that the laminae in the sediment have deformed plastically downwards into the body cavity, but that the laminae are truncated (arrowed). The truncation must have predated the plastic deformation and occurred as the fish penetrated the sediment; $\times c. 1.5$.

the sediment at the same angle. If the mouth was open, sediment filled the buccal cavity and spread over the gill arches and invaded the gill filaments. During penetration, the velocity reduced, due to friction and the change in density contrast, and the fish carcass would have come to rest. Decomposition of the soft tissues occurred, with the resultant gases bloating the carcass, and soft tissue phosphatization commenced in some specimens. If the overall density of the fish carcass



TEXT-FIG. 13. A, longitudinal cross section through cf. *Rhacolepis* sp. (UOP 96/6), showing a gut filled with three-dimensionally preserved crustaceans in which soft tissues have been replaced by calcium phosphate (arrowed). $\times c$. 1. B, detail of crustacean, probably a decapod, showing well-preserved appendages (arrowed). Once again, the presence of stomach contents in good condition indicates that the fish penetrated the sediment very shortly after death, or perhaps even while still alive; $\times c$. 10.

decreased with the build-up of gases, some reverse movement may have occurred, but would have been minimal due to the braking action of the backward-pointing scales and fins. As gas pressure built up and the body wall weakened due to continued decomposition, the gas may have burst through the body wall and invaded the surrounding sediment, leaving a trail of disturbed laminae. The loss of gas allowed the confining sediment to collapse the body wall, sometimes bringing both sides together.

Decomposition of the soft tissues continued and liberated elements of the axial skeleton, small components of which fell geopetally within the body cavity. Any rupturing of the body wall allowed the ingress of sediment. The clay rich sediment may have behaved plastically, flexing into cavities rather than flowing. The proliferation of sedimentary bacteria and resultant early lithification, by calcite, of the surrounding sediment halted further collapse of the body wall. Soft tissue decomposition was probably completed after only a few weeks (Martill and Harper 1990). Commencement of calcite cementation on to all internal surfaces, including skeletal elements, probably occurred at an early stage and may have accompanied some soft tissue decomposition (Briggs and Wilby 1996). Precipitation of calcite resulted in cementation of ingressed sediment within the body cavity of the fish. Calcite also crystallized poikilotopically within the phosphatized soft tissues. Septarian cracking of the larger concretions was probably also an early event, as has been demonstrated for early diagenetic concretions in some black shales (Martill and Hudson 1989). Later calcite cements remain to be dated, but some fill septarian cracks as well as lining larger

vuggy cavities within the fishes. At an even later stage baryte and celestine filled some of the remaining cavities, although not in all concretions, suggesting perhaps that there is geographical and stratigraphical control on their distribution. Finally, compaction of sediment surrounding the concretion occurred, usually resulting in compression of any elements of the fish skeleton that projected beyond the limits of the concretion. It should be noted that the fish were introduced into a medium in which diagenetic reactions were already taking place. Most probably, the fish penetrated into the zone of sulphate reduction, as pyrite is present as a very early phase. Locally, bacterial activity within the sediment would have been increased by the sudden addition of abundant nutrients, thus fuelling further diagenetic reactions, including concretion formation.

SUBSTRATE CONSISTENCY

The lack of bioturbation in the Romualdo Member concretions, and the presence of millimetric scale lamination might seem inconsistent with the former existence of a soupy substrate. Rhoads (1970) noted that soupy substrates are often generated by the accumulation and bioturbation of faecal pellets by infaunal deposit feeders. This has been observed in Recent tidally dominated mud systems (Rhoads 1970) and has also been claimed for Jurassic organic-rich mudrocks, such as the Peterborough Member of the Oxford Clay (Hudson and Martill 1991). So, can soupy substrates be produced without bioturbation? Unconsolidated sediments can exist in three physical states: fluid plastic or soft, and firm bonded. The physical state is controlled by, amongst other things, the water content. For a dead fish to have penetrated the sediment, the sediment must have behaved in a fluid manner at the point of impact. The liquid limit for clays is highly variable, but commonly occurs at water contents of around 135 per cent., while the water contents of sediment at the sea floor may be around 190 per cent. (Skempton 1970). However, when water contents are lower, sediment can still behave in a fluid manner if pore water pressure is increased locally, as for example when an object impacts with it.

As soon as a descending fish hit the sediment the impact shock-wave caused disintegration of weak inter-clay particle bonds allowing the clays to behave in a fluid manner. This was especially marked at the sediment surface, and a zone of homogenous sediment, the result of liquefaction, is better developed at higher levels within the concretions (Text-fig. 5). Liquefaction of the sediment is also more marked just anterior to the skull, at the impacting site. In all cases, the zone of liquefaction surrounding the fish is narrow (rarely more than 10 mm thick), all lamination is disrupted, and the sediment has become homogenized. In some specimens, the zone of homogenized sediment adjacent to the body wall in the middle of the trunk where the sides are almost parallel is absent. In this region the laminae appear to have been sheared (Text-figs. 4A).

The depth of the zone in which the sediment could be liquefied may have been variable within the basin. In the largest known specimen in which the entire fish has entered the sediment it had penetrated to a depth of 250 mm (Text-fig. 2). After penetration, the sediment could become plastic, as ageing allowed new clay bonds to be produced. This probably occurred relatively rapidly, since in some cases plastic deformation of the surrounding sediment can be seen where body wall collapse has occurred and laminated sediment has filled the space without entering the fluid phase (Text-figs 8, 12).

After impact, excess pore fluid pressures could dissipate and the sediment returned to the plastic state. Evidence for this is found in the Romualdo concretions where the body wall of the fish has parted from the sediment surface to leave a void. The sediment clearly remained largely undeformed except for some slight bending of laminae as the gaps between the sediment margin and the body wall of the fish are now filled with later spar cements (Text-figs 8, 12).

DISCUSSION

Soupy substrates can conceal carcasses from the activities of macroscavengers and allow their rapid introduction into a zone of mineralization. The rich bacterial biota within the 'soup' may profit from the introduced organic matter, resulting in rapid early diagenetic reactions conducive to the

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exceptional preservation of articulated, three-dimensional skeletons, sometimes with preservation of soft tissues. Soupy substrates, or 'soup grounds' can be recognized in the fossil record by a variety of taphonomic features, including fossils occurring at high angles to bedding when this is not likely to be a true-life position and by cross-cutting relationships to laminations. In addition, evidence for very soft sediment may be found in the traces left by gas bubbles that escaped from decomposing carcasses. Soup, grounds can also act as 'store houses', accumulating large numbers of exceptionally preserved fossils over prolonged periods. Thus the Romualdo Member concretions are both a fossil conservation *Lagerstätte* and a fossil concentration *Lagerstätte*.

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DAVID M. MARTILL

Department of Geology Palaeobiology Research Group University of Portsmouth Burnaby Building Burnaby Road Portsmouth POI 3QL, UK

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